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This is the author's manuscript

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1552180 since 2022-12-21T11:24:32Z

Published version:

DOI:10.1007/s10071-016-0961-x

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04 May 2023

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***This is an author version of the contribution published on**:*
Questa è la versione dell'autore dell'opera:
[Animal Cognition, DOI: 10.1007/s10071-016-0961-x]

The definitive version is available at:
La versione definitiva è disponibile alla URL:
[http://link.springer.com/journal/volumesAndIssues/10071]

Evidence suggests vocal production learning in a cross-fostered Risso's dolphin (*Grampus griseus*)

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Acknowledgments

We would like to thank the marine mammal staff of the Oltremare Marine Park, especially Daniele Zanzi and Barbara Biancani. We are also grateful to Giulia Bemporad for help with data collection, Thomas Götz and Volker Deecke for providing helpful comments and Olivier Pierre Friard for technical support. Livio Favaro was supported by the University of Torino through a MIUR PhD scholarship. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

Abstract

Vocal learning is a rare skill in mammals and we have limited information about the contexts in which they use it. Previous studies suggested that cetaceans in general are skilled at imitating sounds but only few species have been studied to date. To expand this investigation to another species and to investigate the possible influence of the social environment on vocal learning, we studied the whistle repertoire of a female Risso's dolphin (*Grampus griseus*) that was stranded at an early age and was subsequently raised in a group of bottlenose dolphins (*Tursiops truncatus*). We show that this cross-fostered animal produced vocal signals more akin to those of its *Tursiops* poolmates than those of Risso's dolphins in the wild. This is one of very few systematic cross-fostering studies in cetaceans, and the first to suggest vocal production learning in the Risso's dolphin. Our findings also suggest that social experience is a major factor in the development of the vocal repertoire in this species.

Keywords Bioacoustics, Bottlenose dolphin, *Grampus griseus***,** Risso's dolphin, Signature whistles, *Tursiops truncatus*

Introduction

Vocal production learning, the ability to modify the acoustic structure of vocalisations after hearing a model sound, is a significant step in the evolution of complexity in communication systems (Janik and Slater 2000). Humans make extensive use of vocal learning to develop speech, but this ability is rare in other animals. Indeed, while many birds are excellent vocal learners, non-human primates and many other mammals are not (Janik and Slater 1997). The only terrestrial, non-human mammals where we find strong evidence for this skill are bats (Knörnschild et al. 2010) and elephants (Poole et al. 2005; Stoeger et al. 2012). However, considerable evidence for vocal production learning can be found in marine mammals (Janik 2014). The best studied species here is the bottlenose dolphin (Richards et al. 1984), where each individual uses vocal learning to develop its own unique signature whistle (Janik and Sayigh 2013). In baleen whales, vocal learning contributes to the development of song (Janik 2014) and pinnipeds have been found to copy sounds of other individuals (Reichmuth and Casey 2014). Despite abundant evidence for vocal learning in a few marine mammals, we still know little about vocal learning in the other species and its role in their social lives. To address these gaps, we investigated whether and how vocal learning can influence the vocal repertoire of a member of a species where learning has not been studied, a Risso's dolphin, that has been cross-fostered by a group of bottlenose dolphins. If vocal learning was important in social integration, we would expect the Risso's dolphin to deviate from its natural repertoire to match aspects of the bottlenose dolphin vocalizations and their use.

Methods

Animal history

In summer 2005, a mother-calf pair of Risso's dolphins was found in the harbour of Ancona (44° 62' N, 13° 50' E), Italy. The calf was a female, approximately 6 months of age. Both animals were transported to a local dolphin facility for veterinary treatments where they were kept in isolation. Nevertheless, the adult dolphin died after two days due to serious health complications. The orphaned calf was kept in quarantine for 30 days and subsequently moved to the Oltremare

marine park in Riccione, Italy. In this new facility, the Risso's dolphin was initially kept with a group of 11 adult bottlenose dolphins (7 males, 4 females). Six of the males were moved to another facility in 2008. At the time of our study in 2011, the bottlenose dolphin group consisted of 1 male, 4 females and a one year old male calf. Three of these animals were caught in the Western Atlantic Ocean over 25 years ago, and moved to Italy from Cuba and the USA. All others were born in captivity in Italy.

Data collection at Oltremare marine park

We conducted behavioural observations on close contact swimming (< 1m) of the Oltremare dolphins over several days from 30 Nov 2009 to 26 Feb 2010. This behaviour is an indicator of a close social relationship in dolphins (Connor et al. 2000). Dolphins were observed as one group (66 hours) or in two groups separated by a gate (32 hours with 2 males separated from the rest of the group). The Risso's dolphin was in the same pools as its preferred social partner, a female named Pelé, in all observation periods. In April 2011, we collected audio and video recordings during 30 different recording sessions over 14 consecutive days. We used an acoustic recording array consisting of four HTI-94-SSQ hydrophones (frequency response 2Hz to 30kHz ± 1dB). The hydrophone output signals were recorded with a Tascam DR-680 digital recorder (sampling rate 96 kHz). During recording sessions, the Risso's dolphin and the bottlenose dolphins were free to swim in the main pool and all four holding pools of the facility. However, we analysed only segments when one animal was isolated from the group by choosing to swim alone in one of three holding pools that we fitted with individual hydrophones. This allowed us to match vocalisations to the emitter by using a time-of-arrival difference analysis of the acoustic signals to hydrophones (Janik et al. 2000). Over the period of recordings, the whistles of the Risso's dolphin were collected in 17 separate sessions, while each of the six poolmates was recorded, on average, in 4 ± 2 (mean ± standard deviation) different sessions.

Acoustic recordings of wild Risso's dolphins

Acoustic recordings in the Canary Islands were conducted continuously on a dispersed 4-hydrophone array, recording to a laptop with an Edirol FA-101 sound card. The acoustic array had 3 hydrophones tensioned to chains at 2 m of depth (2 HTI-96-MIN and one HTI-94-SSQ, frequency response 2Hz-to-30kHz ± 1dB), and a fourth hydrophone at 10 m of depth (SRD hydrophone HS/150, frequency response 1kHz-to-100kHz ± 1db). Recordings were collected for as long as possible in a sea state of 3 or less (Beaufort scale) in dry weather using sampling rates of 96 kHz (33% of recordings) and 192 kHz (67% of recordings). Signal to noise ratio (SNR) was calculated for each of the 115 recorded whistles in a total recording time of 45 hours in the presence of Risso's dolphins. Only 62 of these had a SNR of 6dB or above which was our criterion for inclusion in the analysis.

Acoustic analysis

Audio segments containing whistles were visually selected by inspection of spectrograms (Hanning window, FFT size 512, 100% window width) using Adobe Audition 2.0. For each whistle, we extracted the pitch contour of the fundamental frequency using the beluga toolbox (available for download at: http://biology.st-andrews.ac.uk/soundanalysis/) for MATLAB®. From each whistle contour extracted with beluga, we measured the following 12 acoustic parameters using automatized procedures in MATLAB®: start frequency, end frequency, minimum frequency, maximum frequency, mean frequency, frequency range (maximum − minimum), duration, time to minimum frequency, time to maximum frequency, number of inflections in the contour (i.e. any change of slope from positive to negative or vice versa), number of steep sections in the contour (i.e. frequency change > 500Hz between one point and the following), and number of steps in the contour (i.e. steep sections preceded or followed by at least 25 ms of frequency modulation of less than 100 Hz).

Statistical analysis

After parameter standardization, we performed a principal component analysis (PCA) on all acoustic parameters using an orthogonal varimax rotation. The PCA reduced the original set of

127 acoustic measurements to a new set of uncorrelated principal components (PCs). The scores of
128 these PCs were then used to calculate pairwise Euclidean distances for each whistle of the Risso's
129 dolphin with those of the captive bottlenose dolphins and wild conspecifics. All analyses were
130 performed in SPSS v. 20 (SPSS, Inc. 2010).
131
132 **Results**
133 Each of the bottlenose dolphins primarily used one individually distinctive and unique signature
134 whistle when swimming alone (time analysed = 01 h 15 m 59 s; $N_{whistles}$ = 151 (8-40 per animal))
135 (Fig. 1a). The cross-fostered Risso's dolphin also produced only one unique whistle type (Fig. 1b)
136 when swimming in isolation (time analysed = 02 h 54 m 24 s; $N_{whistles}$ = 192), similar to the use of
137 signature whistles found in bottlenose dolphins. Descriptive statistics of the whistle parameters for
138 this type are presented in Table 1a. Interestingly, recurring whistle contours in our sample of wild
139 Risso's dolphin whistles were rare (Fig. 1c) (time analysed = 45 h; $N_{whistles}$ = 62).
140
141 The PCA reduced the 12 acoustic parameters measured from the fundamental frequency to
142 four independent PCs. These four components explained 81.93% of the total variance (PC1 =
143 24.56%, PC2 = 22.88%, PC3 = 19.82%, PC4 = 14.68%). Table 2 shows the factor loadings for
144 each principal component. In particular, the main separating PC (PC1) represented primarily
145 maximum frequency, mean frequency, frequency range, duration and time to maximum frequency.
146 In the space defined by PC1-PC2 and PC1-PC3, the signature whistles of the Risso's dolphin
147 made a distinctive cluster within the range of variation of bottlenose dolphin vocalisations, and they
148 were separated from the cluster made by whistles from wild conspecifics recorded in the Canary
149 Archipelago (Fig. 2). Mean Euclidean distances indicated that similarity is higher between the
150 whistles of the captive Risso's dolphin and those of the bottlenose dolphin (2.870±0.004; mean ±
151 SE pairwise distances) than to whistles of wild conspecifics (3.074±0.009). Interestingly, the
152 whistle parameters of the Risso's dolphin whistle most closely matched those of an adult female
153 (Pelé) that she spent most of her contact time with (time spent at more than 1 m from conspecifics:
154 74%, time close to Pelé only: 15%, time close to other dolphins: 11%) and those of the one adult

155 male that stayed in the pool for the whole study period even though she was not observed to
156 interact with him.
157
158 **Discussion**
159 The evidence presented here suggests that Risso's dolphins are capable of vocal learning. We
160 analysed the whistle repertoire of a female that became orphaned at an early age and grew up in a
161 community of captive bottlenose dolphins. We found that the cross-fostered Risso's dolphin
162 produced almost exclusively one whistle type when in isolation, similar to the use of signature
163 whistles found in bottlenose dolphins (Janik and Sayigh 2013). Interestingly, recurring whistle
164 contours in our sample of wild Risso's dolphin whistles were rare. Together with the very low
165 whistle rate we found for wild Risso's dolphins in the Canary Islands, this may indicate an absence
166 of signature whistles in wild Risso's dolphins. However, Risso's dolphin behaviour in the Canaries
167 may differ from that in other geographic locations. A signature whistle has been found in one other
168 captive Risso's dolphin but this animal was also housed with bottlenose dolphins (Caldwell et al.
169 1969).Killer whales have also been found to change their vocal behaviour when housed with
170 bottlenose dolphins (Musser et al. 2014), further supporting the importance of the social
171 environment for repertoire development in delphinids. It remains to be seen whether Risso's
172 dolphins use signature whistles when with conspecifics.
173
174 Overall, our results show that the whistles of the cross-fostered Risso's dolphin were much
175 closer to those of its bottlenose dolphin pool mates than to wild Risso's dolphins from the Canary
176 Islands (Figure 2). This was also confirmed by the analysis of Euclidean distances, chosen as a
177 similarity measure. While the Canary Island population may differ from Risso's dolphins in the
178 Adriatic Sea, a comparison of our data with published data from wild Risso's dolphin from the
179 Azores and from Scotland (Rendell et al. 1999) also suggests that the cross-fostered individual
180 used its pool mates as a model for its whistle. Table 3 shows that average values for start, end,
181 minimum, maximum, and mean frequency of the captive Risso's dolphin whistles were
182 considerably closer to the average bottlenose dolphin whistles from its pool than to those from

these other conspecific populations. Little is known about wild Risso's dolphin vocalizations and their social organization appears to be different from that of well-known vocal learners like bottlenose dolphins or killer whales (*Orcinus orca*) (Hartmann et al. 2008). Risso's dolphins live in relatively stable, non-matrilineal groups. Thus, it is difficult to speculate how Risso's dolphins would use vocal learning in the wild.

In conclusion, our results provide evidence that the cross-fostered Risso's dolphin developed a signature whistle and used overall whistle parameters that were more similar to bottlenose dolphins than to those used by wild Risso's dolphins. Cross-fostering is one of the few strong approaches to the study of vocal learning and as shown here can add information on the role of social partners in its usage. Our study only describes one animal and can therefore only suggest the influence of vocal learning on whistle development. Changes in vocalizations could be achieved through copying as in vocal production learning, or through selection of pre-existing vocalization patterns as would be the case in contextual learning. The large differences in parameters, especially in start frequency and frequency range, between the cross-fostered animal and the three wild populations of Risso's dolphins suggest that this is a case of vocal production learning. However, future studies need to address the role of signature vocalizations in this species as well as the mechanism of learning with a larger sample size.

201

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Tables

Table 1. (a) Descriptive statistics of whistle parameters. (b) Mean values and standard deviation of whistle parameters from captive bottlenose and Risso's dolphins and wild Risso's dolphins recorded in the Azores and Scotland by Rendall et al. (1999). Shaded boxes indicate parameters in which the cross-fostered Risso's dolphin was more similar to the captive bottlenose dolphins than to the wild Risso's dolphins.

		Start frequency (Hz)	End frequency (Hz)	Minimum frequency (Hz)	Maximum frequency (Hz)	Mean frequency (Hz)	Frequency range (Hz)	Duration (ms)	Time to minimum frequency (ms)	Time to maximum frequency (ms)	Number of inflections in the contour	Number of steep sections	Number of steps in the contour
(a)													
Risso's dolphins recorded in the Canary Archipelago (n=62)	Mean	11461	12810	10094	15205	12471	5110	506	228	298	1	1	0
	St.Dev.	2781	4310	2476	3932	2823	2976	220	248	248	2	2	2
Cross-fostered Risso's dolphin (n=192)	Mean	6006	7769	5771	16852	12372	11080	757	95	615	1	2	2
	St.Dev.	1015	1300	872	1474	852	1708	114	239	117	0	1	1
Bottlenose dolphin Pelé (n=26)	Mean	6748	6863	5165	19080	11283	13915	432	360	252	3	10	7
	St.Dev.	833	1179	1116	1515	926	1450	100	152	172	1	4	3
Bottlenose dolphin 2 (n=40)	Mean	8276	9680	6187	9952	7014	3764	130	16	181	1	2	1
	St.Dev.	600	894	139	1002	339	984	34	9	114	0	1	0
Bottlenose dolphin 3 (n=8)	Mean	8818	10635	4471	10635	7048	6164	1353	712	231	2	4	3
	St.Dev.	380	814	1ß28	814	204	752	130	49	432	1	3	2
Bottlenose dolphin 4 (n=27)	Mean	16115	6620	6576	17688	10941	11111	539	500	39	1	1	1
	St.Dev.	1248	110	124	982	299	984	46	50	16	1	1	1
Bottlenose dolphin 5 (n=28)	Mean	6862	13110	6034	15407	10023	9373	701	232	461	3	7	5
	St.Dev.	1572	3799	1247	2668	1467	2788	155	250	181	1	4	3
Bottlenose dolphin 6 (n=22)	Mean	9096	5380	5214	11150	7385	5936	788	729	82	1	1	0
	St.Dev.	1605	347	344	1737	647	1577	132	123	55	1	1	1
(b)													
Risso's dolphins recorded in the Azores (n = 82)	Mean	12100	10830	8830	13440	11300	4610	530					
	St.Dev.	2160	3330	2710	2690	2290	2680	260					

and Scotland (n = 1182)								
Cross-fostered Risso's dolphin (n=192)	Mean	6006	7769	5771	16852	12372	11080	757
	St.Dev.	1015	1300	872	1474	852	1708	114
Oltremare bottlenose dolphins (n = 151)	Mean	9258	8611	5819	14129	9065	8309	521
	St.Dev.	3507	3149	940	3998	2011	4024	324

Table 2. Results of the principal component analysis with varimax rotation. The table shows factor loadings of the acoustic parameters on the principal components showing eigenvalues > 1 (PC1-PC4) extracted from the PCA. Bold text indicates the largest factor loadings ($r > 0.5$).

Acoustic parameter	Principal Component			
	1	2	3	4
Start frequency	-0.072	-0.269	**0.529**	**-0.728**
End frequency	0.009	0.124	**0.831**	0.210
Minimum frequency	0.098	-0.283	**0.885**	0.180
Maximum frequency	**0.879**	0.317	0.194	-0.043
Mean frequency	**0.877**	0.014	0.376	0.119
Frequency range	**0.742**	0.442	-0.312	-0.061
Duration	**0.614**	-0.049	-0.475	-0.048
Time to minimum frequency	-0.014	0.020	-0.285	**-0.852**
Time to maximum frequency	**0.644**	0.070	-0.179	**0.627**
Number of inflections in the contour	0.086	**0.720**	0.001	-0.058
Number of steep slope sections	0.126	**0.952**	-0.044	0.040
Number of contour jumps	0.157	**0.921**	0.077	-0.105

Figure Captions

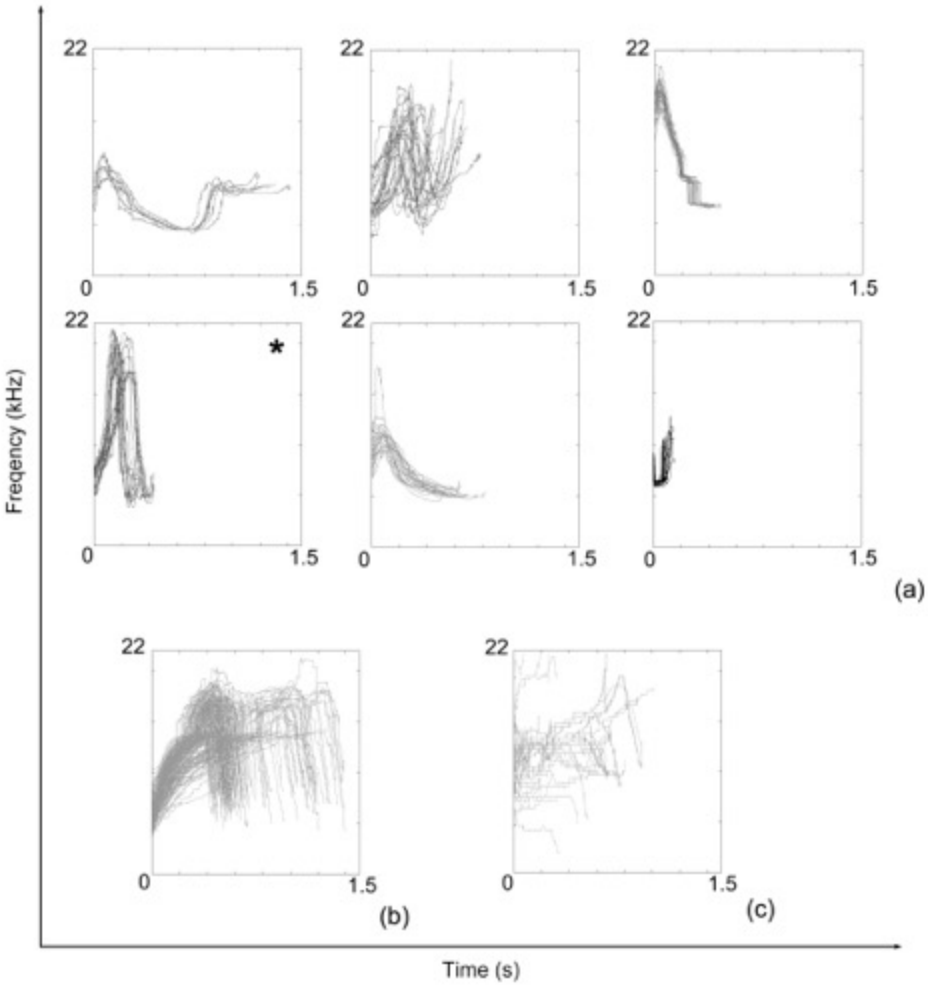

Fig. 1 Pitch contours extracted for the signature whistles of the six bottlenose dolphins (a; * indicates the whistles of Pelé) and the Risso's dolphin (b). The contours of the whistles recorded from wild Risso's dolphins in the Canary Archipelago are presented as a comparison (c)

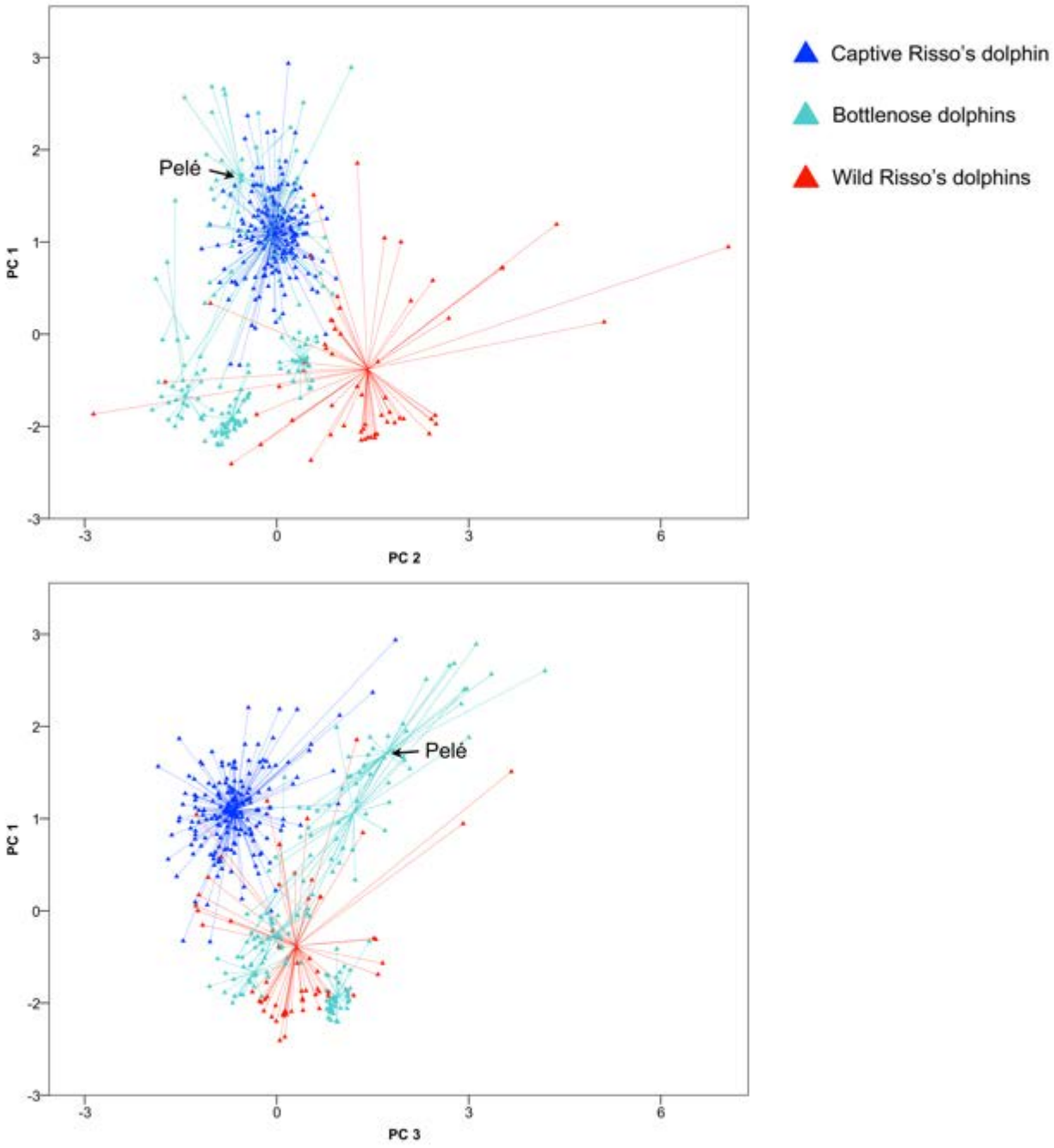

Fig. 2 Whistles plotted in the space defined by principal components. The signature whistles of the captive Risso's dolphin made a distinctive cluster within the range of variation of bottlenose dolphin vocalisations, which was separated from the cluster made by whistles from wild conspecifics